

Hind wing venation of Coreidae (Heteroptera) : a history of misinterpretation

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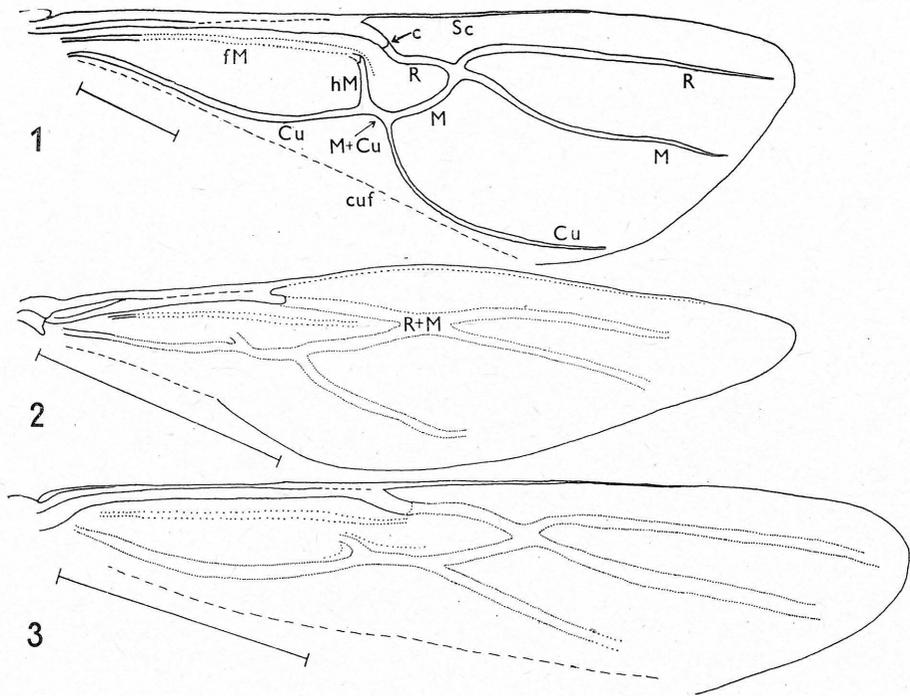
Several features of the hind wing venation were used — from Stål (1867) to Schaefer (1965) — as important distinguishing characters between the coreid subfamilies Coreinae and Pseudophloeinae (= Arenocorinae) and were employed for considerations on the taxonomic position of the genus *Spathocera* Stein, 1860 (= *Atractus* Laporte, 1832 nec Wagler, 1828)* as well. Unfortunately, misunderstanding of classical morphological terminology has caused a series of curious shifts in the meaning of chief diagnostic characters in the most important recent papers concerning Coreidae (China & Miller, 1959, Schaefer, 1965). The purpose of the present paper is to elucidate the situation by illustrating the hind wing venation in a few representative species of both subfamilies and then to follow the history of interpretations of its diagnostic features. This history is being written not to blame the outstanding authors mentioned above but to show how it might have happened that the large and well known subfamilies are characterized in serious modern works by entirely wrong characters. In this respect the case is very instructive.

Remigium of Coreinae and Pseudophloeinae

The following account refers to the structure of the anterior lobe (= remigium) of the hind wing as studied in six selected illustrated species. Discussion is to be found at the end of the paper.

The proximal part of the costal margin is formed by closely joined and fused Sc and R which are, however, still recognizable and in *Phyllomorpha laciniata* (Fig. 2) distinctly separated at the base. Sc is atracheate and, after the divergence or R, remains in marginal position, gradually disappearing and forming a marginal couple; it is best developed in *Phyllomorpha*. An elongate closed field is anteriorly delimited by R, which always bears a caesura (defined by Leston, 1953) after the divergence from Sc; posteriorly the field is delimited by a composite vein formed by Cu, M+Cu and M successively from base to apex (Fig. 1). R, M and Cu run as free veins distally to the field; R and M arise from the apex of the field at the same point, or they may form (Figs. 2,4) a short common branch R+M; in *Spathocera*

*) *Spathocera* appears in various classifications either in Coreinae or in Pseudophloeinae and it has even been included (Wagner, 1966) in a separate subfamily. Its position will be discussed elsewhere in connection with revision of the genus *Haidara* Dist. (Linnavuori & Štys, in prep.); here the genus is considered as of incertae sedis.

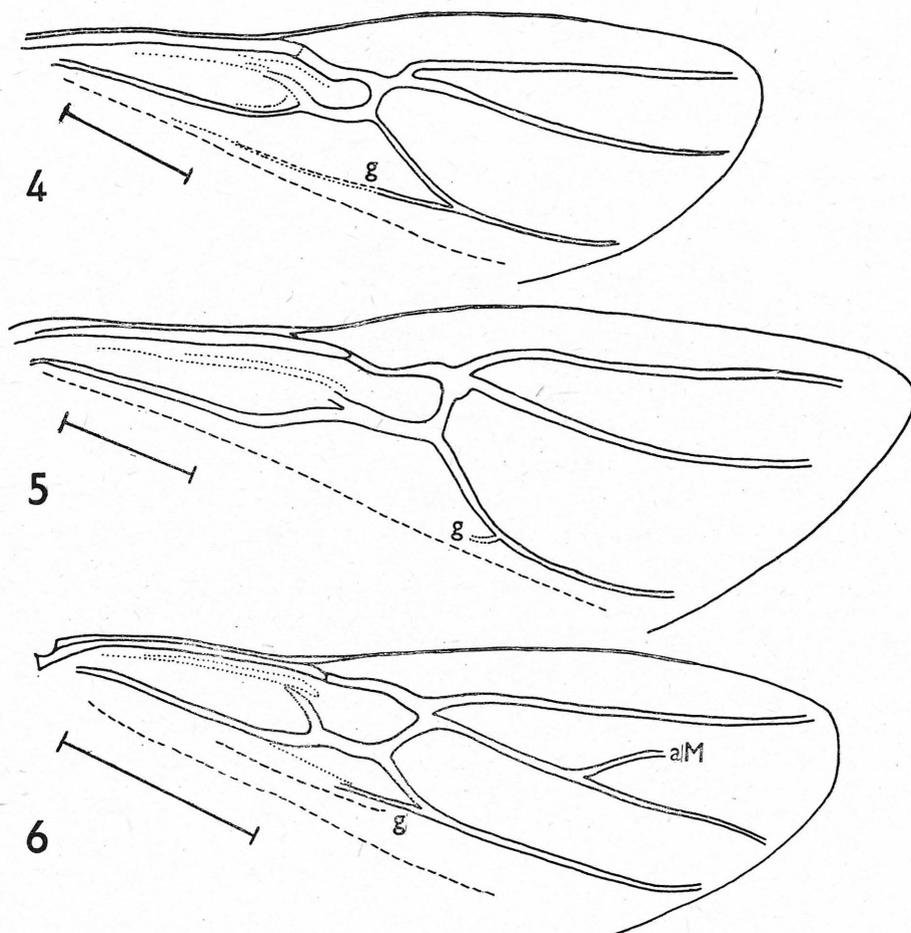


Remigium without glochis. Fig. 1 — *Coreus marginatus* (L., 1758), Coreinae: Coreini. Fig. 2 — *Phyllomorpha laciniata* (Villers, 1789), Coreinae: Phyllomorphini. Fig. 3 — *Pephricus fragilis* Distant, 1901, Coreinae: Phyllomorphini.

Lettering: c = caesura, cuf = anterior branch of the cubital furrow, fM = medial fold (= original track of M?), hM = sector of M forming the hamus. Scale = 1 mm.

laticornis the distal sector of M has sometimes an adventitious anterior branch (Fig. 6 — absent on the opposite wing of the specimen figured). The above veins are mostly sclerotized with the exception of Phyllomorphini (Figs. 2,3) in which the sclerotization is limited to Sc, R and extreme base of Cu, the sclerotization of R stopping abruptly at the caesura.

The proximal part of Cu is at about two thirds of the field joined from within the field by a spur-like vein, the hamus, which represents a part of M. The proximal sector of M is absent, the vein being captured by R, but there is a membranous fold parallel to R and running close to it inside the field; it probably represents a remnant of the original track of M and I call it a medial fold. It is universally present, its base is sometimes (Fig. 1) still vein-like and slightly sclerotized, and its apex usually adjoins the apex of the hamus anteriorly, slightly exceeding it. Only in Phyllomorphini (Figs. 2, 3) the medial fold does not appear to have any association with the hamus and extends much more distally than in other species. The hamus is also universally present, but in Pseudophloeinae (Figs. 4, 5) it is only very slightly sclerotized; it is least developed and non-sclerotized in Phyllomorphini (Figs. 2, 3). The apex of the hamus is usually indistinctly delimited.



Remigium with glochis. Fig. 4 — *Coriomeris denticulatus* (Scopoli, 1763), Pseudophloeinae. Fig. 5 — *Ceraleptus gracilicornis* (Herrich-Schäffer, 1835), Pseudophloeinae. Fig. 6 — *Spathocera laticornis* (Schilling, 1829), subfam. inc. sed.
 Lettering: aM = adventitious branch of M, g = glochis (= antevannal vein). Scale = 1 mm.

The free distal sector of Cu is simple in Coreinae, but in Pseudophloeinae (Figs. 4, 5) and *Spathocera* (Fig. 6) it is joined by a seemingly recurrent straight vein which may be represented by a short sclerotized stump only (Fig. 5) or may be long, distinct, gradually towards the base of wing transforming into a membranous fold parallel to Cu. This vein, called glochis by Stål (1867, 1873) and antevannal vein by Leston (1953), is atracheate and might well be the original track of Cu, a remnant of a stage before the vein Cu had captured the sector of M distal to the hamus. This view is also supported by the taxonomic distribution of glochis, since this vein occurs in more plesiomorphic taxa (Pseudophloeinae in Coreidae, Dayakiellinae in Colobathristidae) but is usually absent in the more apomorphic groups.

The remigium is posteriorly delimited by the anterior branch of the cubital furrow; in *Spathocera* (fig. 6) there is another short intervening fold parallel to the glochis. The remigium is rather narrow and pointed in Phyllomorphini (Figs. 2, 3) which show a tendency to stenoptery.

Historical account of the usage of hind wing venation in the diagnostics of Coreinae and Pseudophloeinae

a) Stål and his followers

Stål is the only author who revised the generic taxonomy of Coreidae on a world-wide scale and laid foundations to their suprageneric classification which is still, in its major features, valid and generally accepted. He characterized (1867, 1873) the hind wing venation of Coreinae as "Vena decurrense alarum glochide plerumque destituta, excepto *Atracto*" (= *Spathocera*), and that of Pseudophloeinae as "Vena decurrense alarum glochide instructa", using this character as the first diagnostic feature in his key. Kirichenko (1916), the second important reviser, used the same wording and gave the character the same importance. However, neither of these authors gave any clue to what they understood by "vena decurrens" and "glochis"; the meaning of these terms by Puchkov (1962, translated into Ukrainian) is not clear either. Of the authors subsequent to Stål none re-examined the hind wing venation of Coreidae in a comparative way and some were apparently puzzled by the meaning of Stål's characters and tactfully ignored them: they are for instance not mentioned in the otherwise detailed work by Gulde (1935). In fact, these characters were not needed for distinguishing between the subfamilies concerned when genera of limited faunal regions only were considered.

What Stål actually had in mind is, however, quite clear from the review of classical morphological terminology by Fieber (1861 : 13, 14, Fig. 49), who defined and illustrated Sc plus proximal sector of R as "costa primaria", Cu & Cu+M as "costa subtensa", the sector of M closing the field distally as "costa connectens", the proximal sector of M situated within the field and joining Cu as "hamus", the free distal sectors of R and M as "costa apicalis", the free distal sector of Cu as "costa decurrens", and the antevannal vein adjoining the latter as "glochis". Also in his key (1861 : 55) to the genera of European Coreidae the couplet "Ablaufende Rippe (= costa decurrens, Štys) des Flügels mit Widerhaken (= glochis, Štys)" and "Ablaufende Rippe einfach, ohne Widerhaken" had been used, probably for the first time, as a single key character to delimit the generic complex which was later called Pseudophloeida by Stål (1867) against the rest of the Coreidae s. lat.

The interpretation of Stål's terminology presented above is also supported by the taxonomic distribution of the "glochis", and in this sense it was used by Štys (1964, 1966), who referred to its presence on Cu in Pseudophloeinae and Dayakiellinae (Colobathristidae).

b) China and Miller

In China & Miller's (1959) key to families and subfamilies of Heteroptera of the World the first key character for Coreinae reads "Hind wing cell without hamus", for Pseudophloeinae "Hind wing cell with a distinct hamus". The formulation gives the impression that a new character concerning the hamus has been discovered;

however, an examination of any species of Coreinae would have revealed to the authors the presence of a distinct hamus. China & Miller actually accepted Stål's (1867, 1873) character concerning the glochis, without re-examination, and erroneously regarded the glochis as identical with the hamus. Apparently they were misled by believing that Stål must have meant the hamus, since the presence, absence or position of this vein is a character often exploited in the higher classification of Heteroptera (e.g. in Anthocoridae), while the glochis had been forgotten by taxonomists except for Leston (1953), who noticed its presence in Pentatomoidea (as antevannal vein).

c) Schaefer

Schaefer (1965) revised the suprageneric classification and phylogeny of the coreoid families; his work is based for the most part on the comparative study of abdomen and genitalia, but he re-examined the hind wing venation as well, and often used various characters of the hamus for characterizations of the tribes Coreidae. He noticed the presence of the antevannal vein (p. 44 "What appears to be the homolog of the pentatomoid antevannal vein is slightly developed in some coreids"), but did not pay more attention to it, not having realized that this is the glochis of Stål which should have a high diagnostic value. On the other hand, he thought (p. 46) that Stål's statement on the presence of the glochis in Pseudophloeinae "appears to refer to the hamus, which, however, is absent in the Pseudophloeinae (Fig. 117) and present elsewhere in the family (the indication of China and Miller (1959) that the reverse is true, is surely a misprint)". Schaefer's Fig. 117 shows, however, the hind wing of *Coriomeris denticulatus* with the hamus present and extending up to the base of the wing; despite this he asserts (p. 44): "If it is true that a hamus extended toward the wing base represents the generalized condition, the Phyllomorphini are the most generalized of the Coreidae in this character. Here the hamus reaches completely to the base. In the Pseudophloeinae, on the other hand, the hamus is lacking altogether (Fig. 117), a condition that seems highly derived and occurs nowhere else in the Coreoidea".

I have re-examined and illustrated (Figs. 3, 4) the wings of the species of Pseudophloeinae and Phyllomorphini studied by Schaefer; it appears that neither the hamus is absent in Pseudophloeinae (as stated by Schaefer in text) nor extended toward the wing base (as shown in his Fig. 117), nor is the latter condition true for Phyllomorphini.

How could it happen that just this and only this part of Schaefer's fundamental paper is so burdened with errors and contradictory statements? There is a logical explanation, the source of confusion being Stål's glochis again.

1. Schaefer unfortunately accepted China & Miller's (1959) erroneous identification of Stål's glochis with the hamus. Since both Stål and China & Miller asserted that seemingly the same structure was lacking in Coreinae (in which the hamus is usually well visible at first glance) and present in Pseudophloeinae (in which it is actually little sclerotized and difficult to see), Schaefer assumed that a lapsus calami or misprint were involved, that Stål and China & Miller wanted to state just the opposite of what was printed in their papers and took the non-sclerotized hamus in Pseudophloeinae for "hamus absent".

2. Schaefer did not notice the distinctness of the hamus and the medial fold. What he has figured in his Fig. 117 for *Coriomeris denticulatus* and what contradicts

so much his text is actually hamus & medial fold. But since the structure is not sclerotized, and the species belongs clearly to Pseudophloeinae, the hamus is "absent". What he refers to concerning Phyllomorphini, must be again the hamus & medial fold. But because the tribe belongs to Coreinae, and although the structure is not sclerotized, the hamus "reaches completely to the base" (of wing).

It is true that both the medial fold and the hamus are rather difficult to see and to characterize: both are little or not sclerotized in the taxa concerned, Phyllomorphini and Pseudophloeinae. The psychological conditioning outlined above may then become important in interpretation.

The diagnostic value of hamus and glochis in Coreidae.

After the description of the actual construction of the remigium in Coreidae and clearing of the errors concerning the hamus and glochis found in literature, we may now consider the diagnostic value of the above structures. It follows from Schaefer's (1965) work that the length, shape and relative position of the hamus can be used as a feature of secondary importance for characterizations of coreid tribes. Employment of this character is, however, obviously limited by difficulties in its objective description since its apex is usually not sharply delimited, and the type of its association with the medial fold (which might be of a rather high phylogenetic significance) is difficult to see and may be easily subjectively misinterpreted. No feature of the hamus in Pseudophloeinae can be used as a primary diagnostic character of this subfamily since a non-sclerotized hamus occurs in Phyllomorphini as well.

A more valuable character is probably the presence or absence of the glochis. The glochis is found in all the Pseudophloeinae which I have examined, and in *Spathocera* Stein (subfam. ?); I have not seen it in any species of Coreinae. On the other hand, Stål (1873) characterized Coreinae as "...glochide plerumque destituta", and Schaefer (1965) showed the presence of glochis in *Galeasis hasticornis* (Thunberg, 1784) (Coreinae: Dasynini) — it may be significant that he demonstrated also a unique type of branching of Cu on corium in the same species. Since the presence of glochis seems to be a highly plesiomorphic character, all cases of its occurrence in Coreinae should be carefully checked and the taxonomic position of the respective species re-investigated.

The remigium of Phyllomorphini has a unique combination of plesiomorphic (well retained Sc which is partly separated from R, medial fold distally strongly exceeding hamus) and apomorphic (stenoptyery, desclerotization of veins, stub-like hamus dissociated from the medial fold, absence of glochis) features. Therefore I completely agree with Schaefer's (1965) opinion reached from different grounds that Phyllomorphini have "a unique combination of advanced and generalized characters and should be considered a separate tribe, if not accorded higher rank", though no formal change of their rank is here proposed.

SUMMARY

1. The main features of the remigium in Coreinae, Pseudophloeinae and *Spathocera* Stein are described; Phyllomorphini (Coreinae) considerably differ from the rest of the subfamily.

2. Tentative homologies of medial fold with the original track of M, and of glochis (= antevannal vein) with the original track of Cu are proposed.
3. Stål's "glochis" is identical with the antevannal vein, not with the hamus, as erroneously supposed by modern authors; their misinterpretations of venational diagnostic characters are reviewed and corrected.
4. Hamus is universally present in Coreidae, and it does not have a diagnostic value at the subfamily level. Pseudophloeinae and *Spathocera* Stein are characterized by universal presence of glochis.

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